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SnapShot: Control of Flowering in *Arabidopsis*

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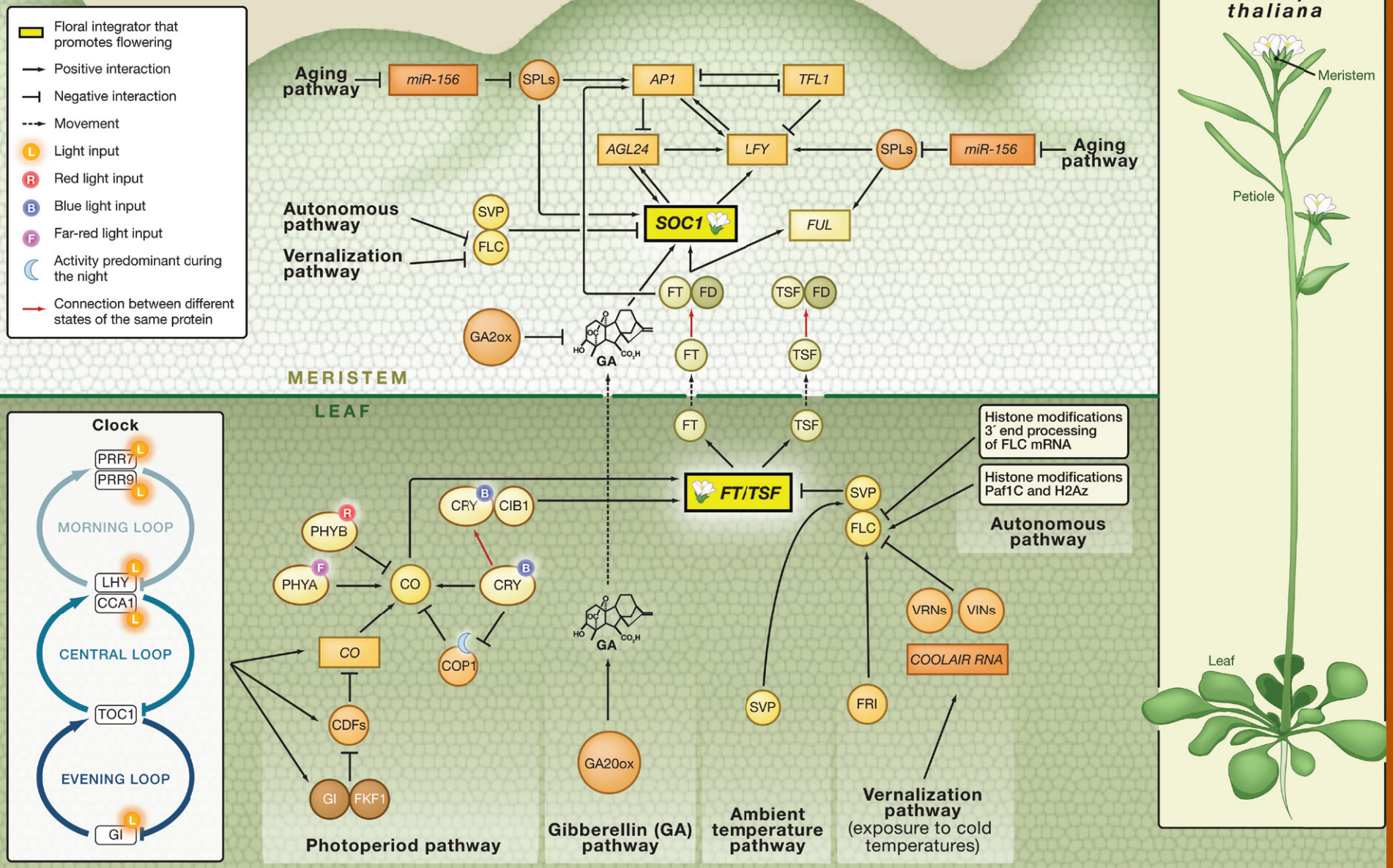

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Plants initiate flowering after a period of vegetative development. During this process, called floral induction, the shoot apical meristem starts to produce flowers instead of leaves. The timing of floral induction is controlled by sophisticated regulatory networks that monitor changes in the environment, ensuring that flowering occurs under conditions most likely to maximize reproductive success and seed production. In the model plant species *Arabidopsis thaliana* ~180 genes have been implicated in flowering-time control based on isolation of loss-of-function mutations or analysis of transgenic plants. This SnapShot presents a subset of these genes and proteins, each organized according to its spatial activity in the leaves or the shoot apical meristem of the plant. Strikingly, several genes act more than once and in several tissues during floral induction. Many of these genes occur in a network of six major pathways: the photoperiod and vernalization pathways control flowering in response to seasonal changes in day length and temperature; the ambient temperature pathway responds to daily growth temperatures; and the age, autonomous, and gibberellin pathways act more independently of environmental stimuli. The six pathways converge to regulate a small number of "floral integrator genes," encoded by different classes of proteins, which govern flowering time by merging signals from multiple pathways. These integrator genes include *FLOWERING LOCUS T* (*FT*) and *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*), which both rapidly promote floral development. In addition, responses to other environmental stimuli, such as the balance of different wavelengths of light or nutrient availability, also influence flowering time, but how these processes interact with the pathways described here is not fully understood.

All genes that we identified from the literature as being implicated in flowering-time control are listed at http://www.mpiz-koeln.mpg.de/english/research/couplandGroup/coupland/floweringgenes/index.html.

Vernalization and Autonomous Pathways

FLOWERING LOCUS C (FLC) is a MADS-box transcription factor that acts as a potent repressor of flowering. Its activity differs among varieties of *Arabidopsis* and is responsible for much of the variation in flowering time observed among these plants. The vernalization pathway activates flowering by silencing *FLC* in response to prolonged exposure to low temperatures. In certain varieties of *Arabidopsis*, cold temperatures trigger antisense transcription at the *FLC* locus, leading to the production of COOLAIR RNA and subsequent silencing of *FLC* transcription. Maintenance of *FLC* repression, even when plants are returned to warmer temperatures, requires histone modifications at the chromatin of the *FLC* locus. These modifications involve the PHD finger protein VERNALIZATION INSENSITIVE 3 (VIN3) and a POLYCOMB REPRESSIVE COMPLEX 2 (PRC2) that includes VERNALIZATION 2 (VRN2).

Photoperiod Pathway and the Circadian Clock

Flowering of *Arabidopsis* is promoted by exposure to long summer days and is repressed by short winter days. The photoperiod pathway controls this response and acts in the leaves through a signaling cascade involving GIGANTEA (GI) and the transcriptional regulator CONSTANS (CO). CO promotes flowering by initiating transcription of the *FT* and *TWIN SISTER OF FT* (*TSF*) genes. During long days, light promotes the interaction between GI and a family of F-box ubiquitin ligases, such as the FLAVIN-BINDING KELCH REPEAT F-BOX 1 (FKF1) protein. These interactions stabilize the F-box proteins, allowing them to promote the degradation of a set of transcriptional repressors of *CO*, including numerous DOF transcription factors called CYCLING DOF FACTORs (CDFs). CDFs repress flowering by downregulating CO expression in leaves. At the posttranscriptional level, CO is degraded in the dark by the ubiquitin ligase CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) and in the morning by a pathway activated by the photoreceptor Phytochrome B (PHYB).

These layers of transcriptional and posttranscriptional regulation ensure that CO activates transcription of *FT* and *TSF* transcription only during long days. Expression and translation of FT occur in the leaves, and the small FT protein then moves through the phloem to the meristem, where it activates the floral development program. Movement of TSF through the phloem may also occur.

The circadian clock is a time-keeping mechanism with a periodicity of 24 hr. The circadian clock confers diurnal patterns of gene expression on ~30% of the genes in *Arabidopsis*. The circadian clock comprises three interlocked feed-back loops. The central loop comprises the partially redundant transcription factors CIRCADIAN CLOCK ASSOCIATED 1 (CCA1) and LATE ELONGATED HYPOCOTYL (LHY), which repress transcription of TIMING OF CAB 1 (TOC1). TOC1 encodes a pseudo-response regulator (PPR) and activates transcription of LHY and CCA1. Similar loops occur in the morning and evening, which include PRR7/PRR9 and GI, respectively.

Many mutations that impair the circadian clock also alter flowering time. For example, the circadian clock ensures that *CO* transcription peaks late in the day, and GI enhances this peak under long-day conditions. In genotypes where *CO* transcription shifts to earlier in the day, CO activation by light is no longer restricted to long days but also occurs during short days, leading to earlier *FT* transcription and flowering under short-day conditions.

Gibberellin Pathway

Gibberellin (GA) is a growth regulator that promotes flowering in *Arabidopsis*. The GIBBERELLIN 20 OXIDASE (GA20ox) enzyme catalyzes several steps in the biosynthesis of GA by oxidizing a number of precursors. Mutations that reduce this biosynthetic pathway or increase the degradation of GA delay flowering, particularly under short-day conditions. The concentration of bioactive GA (GA_4) increases at the meristem immediately prior to floral induction. This GA_4 probably moves from other parts of the plant to the meristem because mRNAs encoding GA20ox and other GA-biosynthetic enzymes do not detectably accumulate at the meristem. However, such mRNAs do increase in the stalk of the leaves (i.e., the petiole) in response to day length, suggesting that the petioles are one site of GA biosynthesis during floral induction. The GA 2-oxidase (GA2ox) enzyme deactivates GA by hydroxylating it.

Ambient Temperature Pathway

Arabidopsis plants flower earlier when grown at higher temperatures, such as 23°C, than at lower temperatures, such as 16°C. The MADS box transcription factor SHORT VEGETATIVE PHASE (SVP) appears to play a crucial role in this pathway because *svp* mutants are insensitive to changes in ambient temperature and flower early at both temperatures. SVP represses *FT* transcription (and thus flowering) at lower temperatures, but the levels of *FT* mRNA increase at higher temperatures.

Age Pathway

As the plant ages, concentrations of the SQUAMOSA PROMOTER BINDING LIKE (SPL) transcription factors increase. SPLs promote flowering by initiating the expression of several other transcription factors, such as LEAFY (LFY), FRUITFULL (FUL), and SOC1. SPL proteins are negatively regulated by the microRNA miR-156, whose cellular levels are higher in younger versus older plants and progressively decrease as the plant ages.

Meristem Responses

During floral induction, the shoot apical meristem transforms from a vegetative meristem, which forms leaves, to an inflorescence meristem, which forms flowers. During this process the meristem becomes taller and more domed. These morphological changes are associated with dramatic changes in gene expression, including increased expression of *SOC1*, which encodes a MADS box transcription factor. *SOC1* activation occurs rapidly when plants are shifted from short days to long days, but *SOC1* responds to other floral induction pathways as well. For example, it is activated by GA and aging but repressed by vernalization and ambient temperature pathways through direct inhibition by FLC and SVP. Activation of *SOC1* during long days requires FT and may be a direct response to the arrival of FT at the meristem from the leaf. FT initiates flower development by interacting with the bZIP transcription factor FD and directly promoting transcription of the MADS box factor *APETALA1* (*AP1*).

SOC1 activation leads to further changes in gene expression in the meristem as it changes shape and becomes an inflorescence meristem. These include the expression of transcription factors, such as LEAFY (LFY), SPLs, and AGAMOUS-LIKE 24 (AGL24). In the inflorescence meristem, TFL1 (TERMINAL FLOWER 1), a PEBP-like protein (Phosphatidylethanolamine binding protein) that shares high sequence similarity with FT, prevents the upregulation of *AP1* and *LFY* mRNA. This restricts *AP1* and *LFY* expression to cells committed to becoming floral primordia and ensures the maintenance of a pool of undifferentiated cells that sustain indeterminate growth of the inflorescence meristem.

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